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Wolf Selection of Human-Modified Linear Features and Cover Types When Hunting and Killing White-Tailed Deer Fawns

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WOLF SELECTION OF HUMAN-MODIFIED LINEAR FEATURES AND COVER TYPES WHEN HUNTING AND KILLING WHITE-TAILED DEER FAWNS

By

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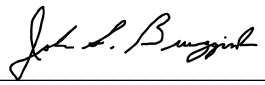

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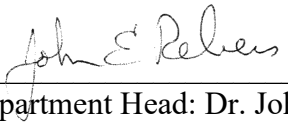

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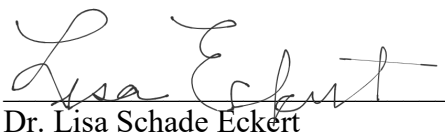

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ABSTRACT

WOLF SELECTION OF HUMAN-MODIFIED LINEAR FEATURES AND COVER TYPES WHEN HUNTING AND KILLING WHITE-TAILED DEER FAWNS

By

Austin T. Homkes

Predators must optimize and adapt foraging behavior for multiple spatial scales to take advantage of abundant and vulnerable prey. Wolves (*Canis lupus*) live in human-modified landscapes where anthropogenic disturbances and landscape alterations can influence predator-prey dynamics. In southern boreal ecosystems, wolves rely heavily on seasonally abundant white-tailed deer (*Odocoileus virginianus*) fawns, which are highly susceptible to predation in their first weeks of life. My objective was to understand how anthropogenic disturbances—specifically timber harvest areas and linear features—and cover types influence where wolves hunt and kill fawns. During 2016–2019, I fit wolves with 20-min-fix-interval Global Positioning System (GPS) collars and searched clusters of GPS-locations to identify where wolves killed fawns. I identified 217 wolf-killed fawns from 12 wolves. I then created 4 models to predict where wolves hunted and killed deer fawns, whether wolves killed fawns in similar places they hunted fawns, and visibility characteristics at kill sites. Wolves hunted and killed fawns near linear features during the early fawning season. Wolves selected young timber harvest areas to hunt and kill fawns but overall hunted farther from these areas. Horizontal visibility (or concealment cover) was lower at kill sites than random sites, which indicated that wolves likely rely on scent to find fawns. By combining wolf movement data, locations where wolves killed fawns, and characteristics of those kill sites, I provide novel insight into how and where wolves forage for fawns in the southern boreal forest.

DEDICATION

To my 7th grade science teacher, Gary Dewey; where the fascination began.

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INTRODUCTION

Predators must adjust their foraging behavior to optimize encounter rates with prey that are seasonally abundant and vulnerable (Torretta et al. 2017). To increase encounter rates with prey, predators must optimize where they forage and for how long (Pyke et al. 1977). Often this is a 2-level selection process because predators must decide not only within which patch to forage (i.e., 2nd order selection, Johnson 1980) but also where to forage within that patch (3rd order selection, Johnson 1980, Lehman et al. 2017). How predators make these decisions is dependent on a variety of factors including variation in prey vulnerability, density, location, and seasonal habitat conditions (Newton et al. 2017).

Wolves (*Canis lupus*) have dynamic diets that shift based on prey availability and season, which requires wolves to shift which patches they use to hunt seasonal primary prey (Gable et al. 2018*a, b*). In the southern boreal forest, wolves travel primarily in packs and hunt adult ungulates such as white-tailed deer (*Odocoileus virginianus*) and moose (*Alces americanus*) in the fall and winter months (Mech 2009, Gable et al. 2018*a*). From spring to early fall, wolf packs raise and provision dependent pups, during which time wolves primarily travel individually and often hunt smaller prey such as beaver (*Castor canadensis*) and even spawning freshwater fish (Benson et al. 2015, Gable et al. 2018*b*, 2020). Such changes in primary prey require shifts in spatial landscape use and therefore foraging behavior (Latham et al. 2013). In late spring, ungulate neonates become available and wolves rapidly shift foraging behavior to take advantage of these newly-abundant and vulnerable, but often hidden prey. Indeed, white-tailed deer fawns

composed >80% of the weekly diet in late-June (Gable et al. 2018*a*) and wolves were responsible for 77% of moose calf mortality in northeastern Minnesota (Severud et al. 2019).

Deer fawns are primarily vulnerable to predation in the first 8 weeks of life (Nelson and Woolf 1987, Rohm et al. 2007). During this time (hereafter referred to as the early fawning season), fawns rely on hiding and cryptic coloration to avoid detection by predators (Nelson and Woolf 1987, Brinkman 2003). Where fawns hide is a two-level selection process that is dependent on both the dam and the fawn (Bowyer et al. 1998, Michel et al. 2020). Parturient dams select summer home ranges to give birth and rear fawns, and fawns select where to bed down within those patches associated with interactions with their dam (Huegel et al. 1986, Demma and Mech 2009, Grovenburg et al. 2012). Fawns generally select bed sites with dense and tall vegetative cover that provide visual concealment from predators (Uresk et al. 1999, Michel et al. 2020). Once >8 weeks old, deer fawns can readily evade wolves, and wolf predation on deer fawns drops precipitously as most fawns reach this age (Gable et al. 2018*a*). To successfully exploit the pulse of available fawns, wolves not only have to identify high-quality habitat patches (i.e., areas with fawns) but also be able to detect fawns when in those patches. In some areas of the southern boreal ecosystem (e.g., northern Minnesota), white-tailed deer are the predominant ungulate species. Thus, in these systems white-tailed deer fawns are the primary prey of wolves during this time (Demma et al. 2007, Gable et al. 2018*a*).

Understanding wolf predation on fawns has remained elusive because of the challenges associated with studying wolf predation during the non-winter period (Palacios and Mech 2010, Gable and Gable 2019). Due to the dense forests in most wolf-deer systems, observing predation events is challenging and, not surprisingly, such observations are rare (Demma et al. 2007). Deer fawns <8 weeks old (weight range = 2.8–3.0 kg) are small prey, and can be almost wholly

consumed by wolves in as little as 20–60 minutes (Voyageurs Wolf Project, unpublished data, Carstensen et al. 2009). Quick handling times by wolves and scant post-feeding remains of wolf-killed fawns make it challenging to identify kills when searching clusters of Global Positioning System (GPS) locations from collared wolves (Palacios and Mech 2010). However, with sufficient training, observers can effectively locate wolf-killed fawns. For example, untrained observers only detected 10% of wolf-killed fawns, but after several weeks of training the same observers detected 100% of wolf-killed fawns (Voyageurs Wolf Project, unpublished data). Such issues have prevented others from studying wolf predation on fawns and other small prey during summer (Demma et al. 2007, Palacios and Mech 2010, Gable et al. 2016, Gable and Windels 2018). However, with extensive observer training and high-frequency GPS-fix intervals, studying wolf predation on deer fawns and other small prey during the summer is possible (Gable et al. 2016, 2018*b*, Gable and Windels 2018).

How wolves hunt fawns is almost certainly different from how they hunt most other prey. As cursorial predators, hunting success of wolves largely depends on their ability to chase and outlast fleeing prey such as adult and juvenile ungulates, which move around the landscape and can effectively flee from wolves once encountered (Mech et al. 2015). In contrast, fawns avoid predators using visual concealment cover and by remaining motionless in their beds to remain undetected. Fawns cannot outrun predators until they are > 8 weeks old (Nelson and Woolf 1987, Rohm et al. 2007). Thus, hunting fawns successfully primarily depends on the ability of wolves to select high-quality habitats (i.e., habitats with fawns) and the ability to detect fawns when in those habitats (Pyke et al. 1977, Johnson 1980).

Because wolves must search for and find motionless fawns, more efficient hunting strategies would also increase encounter rates with fawns. Wolves use anthropogenic linear

features (e.g., seismic lines, power lines, and roads) to increase movement rates, and thereby increase encounter rates with adult prey (Latham et al. 2011, Whittington et al. 2011, McKenzie et al. 2012, Courbin et al. 2014, Dickie et al. 2017). This is especially true when linear features intersect high-quality prey habitat (DeMars and Boutin 2018). Ungulate prey also use anthropogenic features such as roads or areas of timber harvest, which increases the risk of predation near these disturbances (Courtois et al. 2002). Whereas other studies on wolf predation on ungulates suggest that the use of anthropogenic linear features benefits wolves when hunting, no studies to my knowledge have shown that wolves use such hunting strategies when searching for deer fawns.

My goal was to understand wolf habitat selection and use of anthropogenic features during the early fawning season. Specifically, my objective was to understand where wolves hunted and killed fawns in relation to general cover types and anthropogenic features such as roads, trails (hereafter referred to collectively as linear features), and timber harvest areas. I predicted:

1. Wolves hunt and kill fawns closer to linear features than would be expected based on availability during the early fawning season. Previous research has indicated that wolves use anthropogenic linear features to increase movement rates thereby increasing encounter rates with prey (Latham et al. 2011, Whittington et al. 2011, McKenzie et al. 2012, Courbin et al. 2014, Dickie et al. 2017). While these studies have primarily focused on adult ungulates, increasing movement rates would also be advantageous when foraging for largely stationary and hidden prey such as fawns. By hunting near linear features, wolves may not only encounter more fawns near linear features, but also decrease travel time between patches of optimal forage quality.

2. Wolves hunt in areas of recent (≤15 years old) timber harvest during the fawning season and subsequently kill fawns disproportionately in these areas. Areas of silviculture improve forage quality for deer, thus, dams are more likely to use these areas (Alverson et al. 1988, Litvaitis 2001). Additionally, recently harvested areas are often characterized by dense vegetation that is important for fawns when selecting bed sites (Rohm et al. 2007). Thus, wolves would hunt in timber harvest areas because white-tailed deer dams likely use these areas to forage and consequently fawns would be bedded nearby (Bowyer et al. 1998).
3. Horizontal visibility at bed sites, which is a measure of concealment cover (Griffith and Youtie 1988, Poole et al. 2007), where wolves killed fawns would be lower than the horizontal visibility at random locations. Previous studies have shown that fawn bed sites are generally in vegetation that is denser and taller than what is available on the landscape (Uresk et al. 1999, Michel et al. 2020). Thus, it is likely that the horizontal visibility will be lower at sites where wolves kill fawns than what is available on the landscape.

STUDY AREA

The Greater Voyageurs Ecosystem (GVE) is a 1,812-km^2 area located in northern Minnesota and contains the 882-km^2 Voyageurs National Park as well an area south of the park in the Kabetogma State Forest. The GVE's northern boundary is the Minnesota-Ontario border, the western boundary is 20 km east of International Falls, Minnesota and extends 50 km eastward to the western edge of the Boundary Waters Canoe Area Wilderness (Fig. 1; Gogan et al. 2004). The GVE is in the Laurentian Mixed Forest Province (Bailey 1980) and contains 4 major lakes— Kabetogama, Rainy, Namakan, and Sandpoint—that cover a total of 342 km^2. The

GVE's forests are a mix of southern boreal and northern hardwood forest types and are composed of white pine (*Picea glauca*), paper birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), quaking aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*) red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*) (Kurmis et al. 1986). Bog and swamp habitats typically contain black spruce (*Picea mariana*), tamarack (*Larix laricina*), white cedar (*Thuja occidentalis*), and alder (*Alnus* spp.). The forests south of Voyageurs National Park, in the Kabetogama State Forest, are actively logged and therefore are a mosaic of regenerating cuts and are dominated by young aspen (*Populus* spp.) with mature mixed forests and wetlands surrounding these areas (Gable and Windels 2018).

White-tailed deer are common in the GVE with pre-fawn densities prior to 2016 and recent (2016–2019) densities of 2–4 deer/km^2 (Voyageurs Wolf Project, unpublished data, Gable et al. 2017). Moose are relatively rare in Voyageurs National Park (<0.15 moose/km^2) and in the Kabetogama State Forest (<0.05 moose/km^2; [Gable et al. 2017, Windels and Olson 2017]). Wolf densities in the GVE are ~4–6 wolves/100 km^2 in summer with average pack territory sizes of 116 km^2 (Gable et al. 2016).

METHODS

Wolf Capture and Collaring

I captured wolves during spring from 2016 to 2019 using foothold traps. I immobilized wolves with 10 mg/kg ketamine and xylazine using a syringe pole and fit them with GPS telemetry collars (Lotek IridumTrack 1D, Loteck Wireless Inc, Newmarket, Ontario, Canada; Vectronic Vertex, Vectronic Aerospace, Berlin, Germany) that recorded locations every 20 minutes. Once collared, I took morphological measurements, hair samples, blood samples, and

recorded sex and approximate age of each wolf. Once processing was complete, I reversed each wolf with 0.15 mg/kg of yohimbine and monitored the wolf until it was able to walk away on its own strength. All capture and handling of wolves was approved by the National Park Service's Institutional Animal Care and Use Committee (MWR_VOYA_WINDELS_WOLF: Appendix A).

Locating Wolf-Killed Fawns

During 2016–2019, I visited clusters of GPS-locations from wolves fit with GPS-collars to locate kill sites that occurred from April to October. I defined a cluster as $\geq$ 2 consecutive locations (20-min fix interval) that were within 200 m of the first location of a cluster (Gable et al. 2018*b*). At clusters, I systematically searched a 20-m radius around the coordinates of every location in the cluster for evidence of a kill (Metz et al. 2011, Gable et al. 2016). Evidence of a kill bone fragments, hair, teeth, fresh blood, and drag marks. I considered a fawn to have been killed by a collared wolf if: 1) the estimated age of the fawn remains and disturbance were consistent with when a collared wolf was at the site, 2) there was no evidence of predators besides wolves, and 3) there was clear evidence of struggle at the site. I recorded the location of kills, photographed the sites, and collected samples for genetic analysis (e.g., hair, teeth, tissue, or bone).

Model Covariates

I measured the distance from kills and locations to the nearest linear feature using an extensive roads and trails layer I created from previous field work in the GVE over a 6-year period (Poole et al. 2007, Whittington et al. 2011, Severud et al. 2019). The roads and trails layer included dirt and paved roads, recreational trails (ATV trails), snowmobile trails, hiking trails (foot paths), and hunting lanes. The purpose of using a layer of anthropogenic linear features that

included more minor trails (such as foot paths and recreational trails) than previous studies (Gurarie et al. 2011), which often only used road or major linear features, was to capture wolf use of linear features at a finer resolution. Wolves undoubtedly use any anthropogenic linear feature to increase movement rates, not simply those available to vehicles or visible from aerial imagery (Dickie et al. 2017).

I measured the distance from kills and locations to the nearest 0–5-year-old, 6–10-year-old, and 11–15-year-old timber harvest areas. I only examined timber harvest areas ≤15 years old because I was primarily interested in understanding how early successional habitat from timber harvest influenced where wolves hunt and kill fawns. Timber harvest in the GVE generally consists of harvest areas of 5–40 ha, which are clearly visible from aerial imagery. Harvest areas had a minimum of 5% of leave area. Using a combination of aerial imagery from 2000 to 2018 and timber sale records from the U. S. Forest Service, Minnesota Department of Natural Resources, Koochiching County, and St. Louis County, I created polygons for all of the areas of timber harvest in the GVE from 2000 to 2018. This method of identifying harvest areas allowed me to identify the approximate age (within about 1 year) of each harvest area. I made all measurements using QGIS (QGIS, version 3.4.11-Madeira, QGIS Development Team 2019).

To classify the dominant cover type around each location, I used the Coastal Change Analysis Program (C-CAP) 2016 regional land cover map. I created a 500 m buffer around each kill/location and used the LecoS plugin in QGIS to determine the dominant habitat type within each buffer (i.e., habitat that composed the largest proportion of buffer). The cover types I used were deciduous forest, mixed forest, wetland, upland forest, and meadow. For more details on C-CAP cover types, see the Regional Land Cover Classification Scheme. Harvest areas ≤ 15 years old in the GVE were dominated by regenerating aspen stands (*Populus* spp.), which provide

ideal habitat for both dams and fawns (Telfer 1974). Thus, these areas were of particular interest and I further separated this forest type into 4 categories: 0–5-year-old, 6–10-year-old, 11–15-year-old timber harvest areas, and deciduous forest (>15 years). I classified the 3 age classes of regenerating deciduous cover types separately because they change rapidly as they regenerate, and a particular age of regenerating forest could be important for where wolves hunt fawns.

Modeling Approach

My study design did not involve completely random sampling; rather, I purposely selected all points where fawn kills occurred and locations where wolves travels and compared them with random, non-kill or non-movement locations. In this sense, the design is similar to "case-control" studies popular in medicine where researchers must use all available data on rare events, such as patients with a disease, and compare them with random subjects closely matched, in other respects, to the target group. In logistic regression, this non-random design carries the possibility of severe bias in coefficients and probabilities if the sample size for the rare event is low (e.g., n = 10–20), or the control group is not carefully matched. However, it has been demonstrated with simulations that this bias is minimal for large sample sizes (e.g., >100) of the rare events (King and Zeng 2001).

To identify cover types wolves used and their proximity to anthropogenic features when hunting and killing fawns, I created 3 models (Kill Model, Hunting Model, and Kill vs. Hunting Model). Each of these models included the same landscape and cover covariates (description of covariates above). I used my Kill Model to identify the cover types wolves selected to successfully kill fawns. By including distance covariates of kill sites to linear features and harvest areas of different ages, I was able to evaluate whether anthropogenic features were important for wolves when killing fawns. I used my Hunting Model to identify the cover types in

which wolves hunt, and the proximity of wolves to linear features and harvest areas of different ages when hunting. I considered any location that was not at a cluster or a homesite to be a hunting location (see above). By investigating where wolves hunted, I could better understand if anthropogenic features are important for wolves when hunting. To investigate whether wolves hunt and kill fawns in similar cover types and in similar proximities to linear features and harvest areas of different ages I used my Kill vs. Hunting Model. Understanding if wolves forage and kill fawns in similar cover types and proximities to anthropogenic features was important for understanding if wolves are successful in killing fawns where they forage for them. In addition, I created 2 models to compare horizontal visibility at kills with what was available within and among patches (models referred to Within Patch Visibility Model and Among Patch Visibility Model; specifics on these models below).

I used generalized linear-mixed models (GLMM) with a logit link (i.e., logistic regression) and a random effect for wolf (Whittington et al. 2011, Fieberg and Johnson 2015) for each model. I included individual wolves as a random effect to account for the fact that data from individual wolves might not be independent. I normalized and log transformed covariates to meet the assumption of a normal distribution. Variance inflation factors were < 2 for all covariates, which indicated collinearity was not a problem. I carried out my analyses using R version 3.5.2 (R Core Team 2018). I evaluated the importance of individual variables with an $\alpha = 0.05$ and confidence intervals that did not overlap 0.

Kill model.—I compared the habitat characteristics at kill sites with randomly-distributed locations to understand where wolves killed deer fawns relative to what was available. I estimated habitat availability by documenting habitat characteristics at 15 random locations within the territory of a specific wolf for every fawn kill made by that wolf (Lehman et al. 2017,

Torretta et al. 2017). I only used kill sites in my analysis where the fawn was killed prior to 15 July of each year to ensure that the fawn was likely $\leq$ 8 weeks old and therefore unlikely to flee from a predator (Carstensen et al. 2017). Thus, kill locations were almost certainly representative of where fawns bedded prior to being killed.

Hunting model.—I compared the habitat characteristics in areas where wolves hunted during the fawning season (26 May -15 July) with habitats that were available within their territories. Wolves are nearly always hunting when traveling and have highly flexible diets that allow them to take advantage of opportunities to take prey when moving about the landscape (Mech et al. 2015, Gable et al. 2018*b*). Thus, I defined hunting locations as GPS-locations that were >200 m from other consecutive GPS-locations (i.e., GPS cluster locations were removed). To estimate habitat availability, I examined habitat characteristics at 1 random location for every hunting location. Each random location was created within the territory of the corresponding wolf to each hunting location.

Hunting vs. kill model.—I compared habitat characteristics at locations where wolves hunted with locations where they successfully killed fawns. To do so, I compared the habitat characteristics of the kills used in the "Kill Model" with the hunting locations used in the "Hunting Model". The purpose of this model was to evaluate whether wolves hunted (i.e., traveled) and killed fawns in similar habitats and in similar proximities to landscape features used in my models.

Assessing Visibility at Kill Sites

I assessed microhabitat characteristics at kill sites both within and among patches by comparing horizontal visibility at kill sites with locations 50 m away from kills (within patch) in 2016 and with randomly-distributed locations around the territory (among patch) in 2016 and

2017. I used a 30.5 cm x 10 cm cover board, which is about the size of a bedding fawn (Fig. 2; Griffith and Youtie 1988, Alldredge et al. 1991). I placed the cover board where kills occurred, which I assumed to be where the fawn was bedded when killed. I estimated the percentage of the board that was visible from 1 m above the ground (to simulate the perspective of a standing wolf) at 5, 10, and 15 m away from the board in each cardinal direction. I also recorded the maximum distance from the kill site at which any part of the cover board could be seen. I averaged the values from each of the cardinal directions to yield a single estimate for each distance measured. To compare horizontal visibility at the kill site with what was available within the patches, I walked 50 m in each of the cardinal directions from the kill and recorded the same information and averaged values as I did at the kill.

To compare horizontal visibility at kills with what was available throughout a given pack territory (i.e., among patches), I measured visibility as above at 1 random location for each kill within in a wolf's territory during the early fawning season. One of the 7 wolves used in this analysis was not a member of an established pack, but rather moved within the boundaries of several packs. I therefore used the combined area of these pack territories to create random locations for the kills made by this wolf. I only assessed visibility during 2016 and 2017 due to logistical constraints.

Because preliminary analyses indicated that visibility measurements were highly correlated (e.g., Fig. 6; $0.458 < r < 0.831$) I used the maximum distance for my analysis because this was likely the most biologically informative covariate (i.e., the distance a wolf can first see a fawn is likely more important than the proportion of a fawn a wolf can see at a specific distance). I created a GLMM to compare visibility at kill sites to what was available at 1) locations 50 m away from the kill (Within Patch Visibility Model) and 2) randomly-distributed locations across

the broader landscape (Among Patch Visibility Model). I normalized the data using a square root transformation. I used $\alpha = 0.05$.

RESULTS

During 2016–2019, I found 303 fawn kills from 20 different collared wolves. Of those, 217 kills from 12 wolves occurred during the early fawning season (26 May -15 July). The wolves in my analysis ranged from ~1–8 years old (Table 1). The earliest date a wolf killed a fawn was 23 May, with the greatest number of kills occurring during 17 June - 22 June (Fig. 4). Fawns were most often killed between 0800 and 1200, with the fewest kills occurring between 0200 and 0400 (Fig. 3).

The estimated variance attributed to the different wolves (e.g., the random effect) used in my Kill Model, Hunting Model, Within Patch Visibility Model, and Among Patch Visibility Model was 0.0. The estimated variance attributed to the different wolves used in my Hunting vs. Kill Model was 0.023. Thus, the effect of the different wolves on the results of all my models was negligible. However, I still included a random effect for wolf in all my models because wolf seem to be the most likely random variable to affect my data and to demonstrate that wolf did not affect my results.

Kill Model

Fawns were killed closer to linear features (β= -0.311, 95% CI=-0.468– -0.155, P<0.001; Table 2, Figs. 5, 7) and farther from 0–5-year-old harvest areas (β= 0.213, 95% CI= 0.021–0.405, P<0.05) than would be expected based on availability. However, fawns were killed in 0–5-year-old cuts more than would be expected based on availability (β= 1.400, 95% CI= 0.521–2.279, P <0.01; Fig. 8). Wolves did not kill fawns in the other cover types more than would be expected by chance.

Hunting Model

Wolves hunted closer to linear features (β= -0.287, 95% CI= -0.341–-0.247, *P* <0.001; Table 2. Fig. 5) and farther from 0–5-year-old harvest areas (β= 0.168, 95% CI= 0.102–0.207, *P* <0.001) than would be expected based on availability. Wolves hunted in deciduous forests, 0–5-year-old harvest areas, wetlands, and upland forests more than expected based on availability during the early fawning season.

Hunting vs. Kill Model

There was no difference in habitat characteristics between locations where wolves hunted fawns and where they killed them (Table 2, Fig. 5).

Within Patch Visibility Model

The mean percentage of cover board visible at 5 m was 27.2 ± 9.9%, at 10 m was 5.1 ± 4.0%, and at 15 m was 0.1 ± 0.02%. The mean maximum distances at sites where wolves killed fawns and 50 m away from kill sites were 5.4 ± 1.2 m and 5.9 ± 0.9 m respectively (Table 3). Maximum distance was not different between fawn kill sites and locations 50 m from kill sites (β= -0.379, 95% CI=-1.187–0.427, *P*=0.356).

Among Patch Visibility Model

The mean proportion of cover board visible at 5 m was 29.4 ± 7.5%, at 10 m was 6.7 ± 3.1% and at 15 m was 1.3 ± 1.2%. Mean maximum distances at sites where wolves killed fawns and at random locations within wolf territories were 5.8 ± 0.9 m and 8.7 ± 0.9 m respectively (Table 3). Maximum distance was lower at fawn kill sites than at random locations (β=-1.169, 95% CI=-1.749–-0.588, p<0.001; Fig 6).

DISCUSSION

Wolf use of both linear features and recently harvested areas indicates that human disturbed areas are important for wolves when hunting and killing deer fawns during the early fawning season (Telfer 1974, Courtois et al. 2002, Gurarie et al. 2011, Lesmerises et al. 2012, Courbin et al. 2014). My study contributes to and supports the existing body of literature on wolf use of anthropogenic linear features and disturbance by extending this characteristic of wolf hunting behavior to wolf predation on deer fawns. Timber industry practices that create and connect areas of timber harvest with linear features and subsequent maintenance of these linear features for continued timber harvest or recreational use (e.g., hunting) create a connected web of travel corridors and a mosaic of early successional habitats that wolves likely use to increase encounter rates with fawns (Sand et al. 2008, Gurarie et al. 2011).

By using wolf hunting locations and sites where wolves killed fawns I identified both where wolves hunt and where wolves successfully kill fawns during the early fawning season. Whereas the use of wolf locations and the locations of adult ungulates killed by wolves are not particularly novel when studying wolf predation (James and Stuart-Smith 2000), by using this approach to study wolf predation on fawns during the first weeks of life, when fawns are primarily hidden and stationary, I provide the first insights into, and a comparison of, where wolves both search for fawns (where they expect fawns to be) and where wolves successfully kill fawns (where they actually encounter fawns). By comparing where wolves hunt and kill fawns I assessed which cover types and landscape features are important for wolves when hunting and killing fawns. This information has implications for future research on wolf predation on other ungulate neonates in similarly modified southern boreal habitats, wildlife and habitat management, and industries that create human modified habitats (Gurarie et al. 2011).

Whereas other work suggests that young successional habitat created by human disturbances creates both ideal forage conditions for adult deer and hiding cover for fawns (Huegel et al. 1986, Akins and Michael 1999, Courtois et al. 2002, Edenius et al. 2002, Rohm et al. 2007), my work suggests these modified habitat characteristics could be ecological traps for ungulates (Robertson and Hutto 2006). Wolf selection for harvest areas of age 0–5 years for both hunting and killing fawns during the early fawning season suggests that wolves seek out these cover types to find fawns. Though these patches of improved habitat for deer may have benefits for both adult and neonates alike, they also provide patches of concentrated prey that wolves select to improve hunting success.

Interestingly, harvested areas 6–10 and 11–15 years old as cover types were not used by wolves to hunt or kill fawns, nor did wolves hunt or kill fawns near harvest areas of these ages as a landscape feature during the early fawning season. Harvest areas in my study area are primarily composed of regenerating deciduous trees and dense understory that benefit adult and neonate deer. However, regeneration of saplings after timber harvest (primarily *Populus* spp. in my study area) can be rapid and browse can grow above the reach of deer within 2–4 growing seasons (Oswalt et al. 2006, Miller et al. 2009). Thus, harvested areas age 6–10 and 11–15 years old likely provide less forage for dams than stands $\leq$ 5 years old. Because fawns choose bed sites within a general area selected by the dam, fawns are less likely to be found in areas with lower forage quality for dams (Bowyer et al. 1998, Uresk et al. 1999). Wolves' avoidance of hunting or killing fawns in or near these older harvest areas (6–15 years old) is likely a reflection of lower forage quality for deer that results in patches of lower forage quality for wolves.

As I predicted, wolves hunted and killed fawns in close proximity to linear features. This finding corroborates previous work on the importance of linear features to wolves when hunting.

Though previous studies on wolf use of linear features have focused on adult ungulates, which wolves kill using cursorial hunting strategies, I focused exclusively on young fawns that hide motionless and rely on cryptic coloration to avoid predators (Mech et al. 2015, Michel et al. 2020). Sites where wolves killed fawns were seldom on or directly adjacent to linear features, which in my study suggests that wolves do not encounter fawns directly on linear features. They are also unlikely to see hidden fawns at a distance and give chase given the dense vegetation in my study area. Rather, I suggest that wolves use linear features to travel between patches of optimal forage quality (i.e., harvest areas of 0–5 yr), and hunt and kill fawns in those patches, which often have linear features near or in them. My conclusion agrees with Gurarie et al. (2011), who found that wolves preferred recently disturbed (by forest management practices) early successional fragmented habitats that were connected by a network of secondary (i.e., low human use) anthropogenic linear features to hunt moose and caribou (*Rangifer tarandus*) calves, and that wolves do not kill prey directly on linear features but use them to travel.

The cover types in which wolves hunted and killed fawns and the proximity to landscape features (i.e., linear features and areas of timber harvest) when hunting and killing fawns did not differ in my study, suggesting that wolves forage where they expect fawns to be. This result supports my hypothesis that wolves search for and kill fawns in certain cover types and near linear features, providing new insight into wolf hunting behavior. Indeed, I suggest that rather than hunting for fawns by moving randomly on the landscape to encounter hidden prey, wolves select young harvest areas near anthropogenic linear features to both hunt and kill fawns (Gurarie et al. 2011). Given that I derived my results from individual wolves in different packs, my insights into wolf hunting behavior are likely applicable to wolves in similar human modified

landscapes, which characterize much of the wolf's North American, and potentially global, northern range (Gurarie et al. 2011, Lesmerises et al. 2012, Gable et al. 2020).

Though a direct comparison of the cover types wolves use to hunt and kill fawns (Hunting vs. Kill Model) suggested there was no difference in use, my examination of where wolves hunted (Hunting Model) suggested they hunt in cover types they do not use to kill fawns (Kill Model). Indeed, the results from my first 2 models indicated that wolves used deciduous forest, wetland, and upland cover types when hunting fawns but not when killing fawns. This discrepancy is likely attributable to differences in samples sizes. Whereas 221 kill sites (3,255 random locations) used in my Kill Model is a robust sample size of kill sites compared to previous studies, I used 4,790 wolf movement locations (4,790 random locations) in my Hunting Model, which could have increased the model's ability to detect more subtle differences in use of certain cover types. Additionally, this difference in model results may reflect which cover types wolves travel through when moving between areas of optimal forage quality (i.e., cover types that contain linear features) or such areas and homesites (Gurarie et al. 2011).

My cover board results suggested that wolves likely use scent to detect fawns at the within patch habitat scale. Once wolves select patches to hunt in at the home range scale they must then detect prey within patches (Johnson 1980). My cover board analysis indicated that sites where wolves killed fawns have lower visibility (i.e., more concealment cover) than random locations (my among patch scale), yet have similar visibility to the area directly surrounding a kill site (my within patch scale). This suggests that wolves successfully locate fawns in patches of habitat with characteristics that I would expect fawns to select for protection from predators (Grovenburg et al. 2010, Michel et al. 2020). Wolves likely cannot see bedding fawns unless they travel <6 meters from them, therefore wolves likely must search for fawns in patches of

dense vegetation rather than encountering fawns by chance on the landscape (i.e., areas with higher visibility). I derived my results from observers viewing a black and white cover board in a known location. Even in these circumstances the average distance an observer could see even a small portion of a cover board was 5.8 m (SD=3.43). Fawns are cryptically colored and lie motionless, often in dense vegetation and wolves do not know where fawns are bedding until they detect them (Grovenburg et al. 2011, 2012). Thus, wolves likely use senses other than sight and hearing to locate fawns. Even if wolves covered extensive distances to search for fawns, it does not seem plausible that wolves could rely on fawns as prey by first coming into close proximity (<6 m) and then visually detecting motionless hidden prey. Therefore I suggest that wolves first detect fawns by smell. Mech and Boitani (2003) speculated that while fawns might have some sort of masked scent, it is improbable that they are scentless. My results support this speculation as fawns must have an identifiable scent to be located by wolves when in close proximity.

Though my results suggest that wolves use olfaction to detect fawns, the data used for my visibility models have limitations. Visibility was lower in areas where wolves killed fawns, but I cannot infer whether this resulted from wolf hunting behavior or dam and fawn foraging and bed selection. My results are only relevant for describing visibility characteristics of where wolves successfully locate fawns and not for fawns they do not detect. However, given the dearth of insight about how wolves detect fawns at the within patch scale, my results are an important starting point for future research on the topic. I suggest future research focus on locating sites where wolves successfully kill fawns combined with location data of fawns that are not killed by wolves to compare characteristics of these 2 sites. This approach would provide

insight into both wolf predation behavior and deer anti-predator behavior during the early fawning season.

Though predation on fawns by wolves warrants study simply because it is an important yet poorly understood aspect of wolf and deer ecology (Palacios and Mech 2010), information on the topic is relevant to additional aspects of wolf-deer ecology such as climate-driven range shift in deer. Climate change is driving the northward expansion of white-tailed deer range into the boreal region of North America (Dawe and Boutin 2016), a region wolves already inhabit. Concurrently, wolf range continues to expand south into western and midwestern states, a region deer already inhabit. Thus, areas of wolf-deer sympatry continue to grow in both regions of North America. As a result, understanding wolf predation on deer will become increasingly important as areas where wolves prey on white-tailed deer continue to expand into regions with other ungulate prey (Gervasi et al. 2013).

SUMMARY AND CONCLUSIONS

I have demonstrated the importance of anthropogenic linear features and modified landscapes for wolves when hunting and killing fawns. My results have implications for wildlife managers and industries that modify landscapes. Ungulate populations benefit from the creation of early successional habitat, whether created directly for ungulate management or as a byproduct of timber harvest. I suggest that these same modified landscapes and the infrastructure created to support them (anthropomorphic linear features) benefit wolves that are preying on ungulate neonates. Consideration should be given to the costs and benefits to ungulate populations when creating early successional habitat. Special attention should be given to the differences of these impacts for ungulates during different parts of the year (i.e., fawning/calving season vs. winter) to investigate whether the ecological traps these habitats create are seasonal.

My work supports previous suggestions that mitigating the usefulness of anthropogenic disturbances for wolves (i.e., tree-felling and fencing in linear features) and modifying land use practices altogether may be the best method for limiting increased predation risk for ungulates by wolves near anthropogenic features (Wasser et al. 2011, Dickie et al. 2017, Finnegan et al. 2018). Future research should focus on whether such mitigation strategies benefit ungulate neonates in the summer and whether or not the benefits of human modified landscapes for ungulates outweigh the benefits for predators.

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Table 1. Summary of the 12 wolves included in models investigating where wolves hunt and kill deer fawns in the Greater Voyageurs Ecosystem, Minnesota 2016–2019.

Wolf ID	Year	Age (yr)	No. of fawn kills	No. of random kill locations (kill model)	No. of hunting locations (hunting model and hunting vs. kill model)	No. of random hunting locations (hunting model)
V028	2016, 2018	6-8, 8-10	50	750	755	755
V046	2017	1-2	9	135	322	322
V049	2017	1-2	15	225	381	381
V052	2016	1-2	10	150	230	230
V061	2018	1-2	18	270	349	349
V066	2018	2-3	9	135	283	283
V072	2019	5-7	17	255	257	257
V074	2019	3-4	16	240	347	347
V076	2019	4-6	26	390	504	504
V077	2019	2-3	17	255	537	537
V079	2019	6-8	17	255	479	479
V086	2019	1-2	13	195	346	346

Table 2. Results from generalized linear mixed model analysis testing wolf (*Canis lupus*) selection ($\alpha = 0.05$) of cover types and proximity to timber harvest areas and human created linear features when hunting and killing white-tailed deer (*Odocoileus virginianus*) fawns from late May to mid-July of 2016–2019 in Minnesota, USA. The models examine selection for cover types and proximity to human created disturbances as they relate to where wolves kill fawns (Kill Model), where wolves hunt fawns (Hunting model) and where wolves kill fawns compared to where they hunt fawns (Kill Model vs. Hunting Model).

Covariates	Kill Model			Hunting Model			Kill vs. Hunting Model		
	β	95% Confidence Interval	*P*	β	95% Confidence Interval	*P*	β	95% Confidence Interval	*P*
Intercept	-2.970	-3.461, -2.480	<0.001	-0.178	-0.308, -0.039	0.010	3.161	2.660, 3.662	<0.001
Deciduous forest	0.219	-0.315, 0.755	0.421	0.223	0.078, 0.371	0.004	0.070	-0.463, 0.602	0.798
Mixed forest	0.259	-0.306, 0.824	0.369	0.001	-0.144, 0.175	0.993	-0.221	-0.786, 0.344	0.444
Wetland	0.467	-0.190, 1.124	0.164	0.208	0.019, 0.399	0.034	-0.231	-0.887, 0.424	0.489

Upland	-1.452	-3.489, 0.585	0.162	0.437	0.174, 0.718	0.003	1.938	-0.092, 3.968	0.061
Harvest 0 to 5 yr	1.400	0.521, 2.279	<0.01	0.820	0.435, 1.045	<0.001	-0.721	-1.603, 0.161	0.109
Harvest 6 to 10 yr	0.008	-1.099, 1.117	0.988	0.222	-0.068, 0.502	0.133	0.317	-0.776, 1.410	0.570
Harvest 11 to 15 yr	0.223	-0.676, 1.121	0.627	0.084	-0.173, 0.376	0.560	-0.115	-1.009, 0.780	0.802
Distance to harvest 0 to 5 yr	0.213	0.021, 0.405	0.029	0.168	0.102, 0.207	<0.001	-0.062	-0.244, 0.120	0.505
Distance to harvest 6 to 10 yr	-0.102	-0.262, 0.058	0.209	0.017	-0.016, 0.083	0.522	0.062	-0.108, 0.233	0.471
Distance to harvest 11 to 15 yr	-0.046	-0.192, 0.099	0.532	0.030	-0.016, 0.075	0.251	0.085	-0.060, 0.229	0.252
Distance to linear feature	-0.311	-0.468, -0.155	<0.001	-0.287	-0.341, -0.247	<0.001	0.002	-0.145, 0.151	0.970

Table 3. Mean (%) of a 30.5 x 10 cm cover board visible to an observer (1 m about ground level) at 5, 10, and 15 m as well as the farthest distance (m) the board was still visible from random locations and sites where wolves (*Canis lupus*) killed white-tailed deer (*Odocoileus virginianus*) fawns. Random locations for *Among Patch* were randomly distributed in wolf territories. Random locations for *Within Patch* were located 50 m in the cardinal directions from a site where a wolf killed a fawn. Fawn kills occurred from late May to mid-July of 2016–2019 in Minnesota, USA.

	Kill Sites		Random Locations	
	Mean	Standard Deviation	Mean	Standard Deviation
Among Patch				
5 m	29.4	27.6	38.5	25.7
10 m	6.8	11.6	12.1	15.6
15 m	1.3	4.6	3.0	5.9
Max Distance (m)	5.8	3.4	8.7	3.7
Within Patch				
5 m	27.3	27.1	23.7	16.6
10 m	5.1	10.5	6.1	7.1
15 m	0.1	0.4	2.8	8.7
Max Distance (m)	5.4	3.2	5.9	2.6

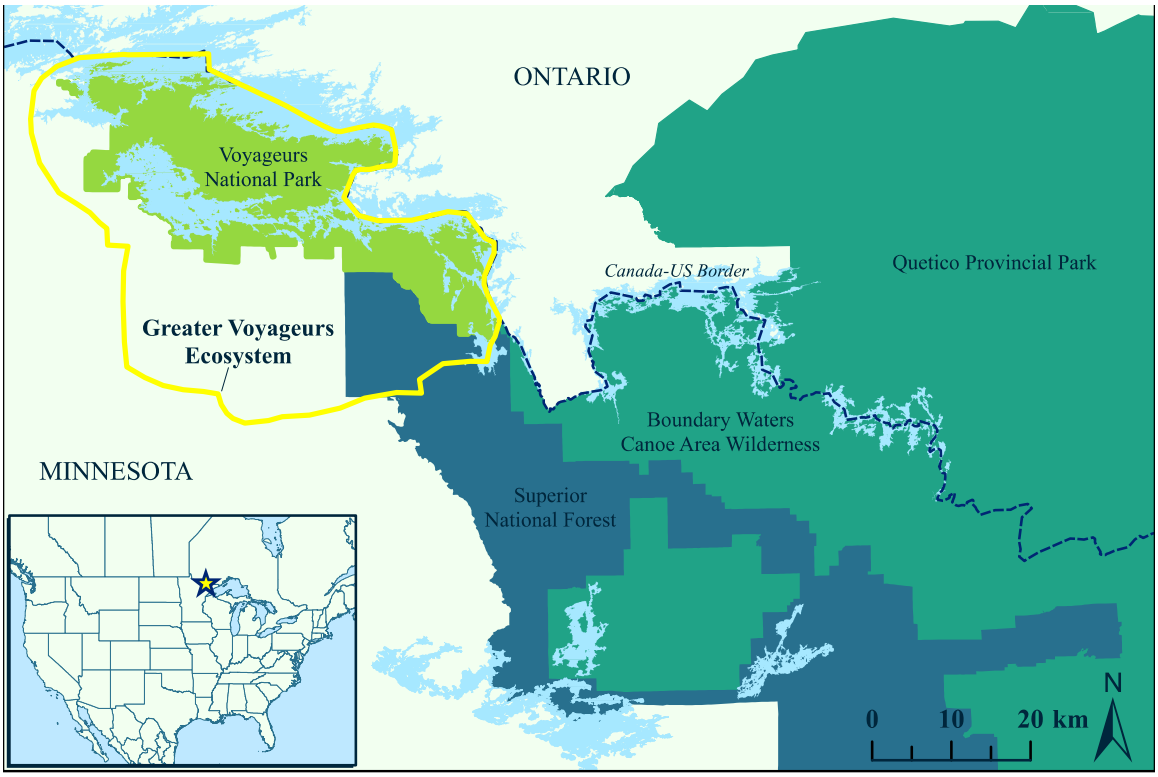

Figure 1. Location of the Greater Voyageurs Ecosystem in northern Minnesota, USA.

Figure 2. A 30.5 x 10 cm cover board used to evaluate horizontal visibility 5, 10, and 15 m as well as at the farthest distance (m) the board could still be seen from random locations and sites where wolves (*Canis lupus*) killed white-tailed deer (*Odocoileus virginianus*) fawns from late May to mid-July of 2016–2019 in Minnesota, USA.

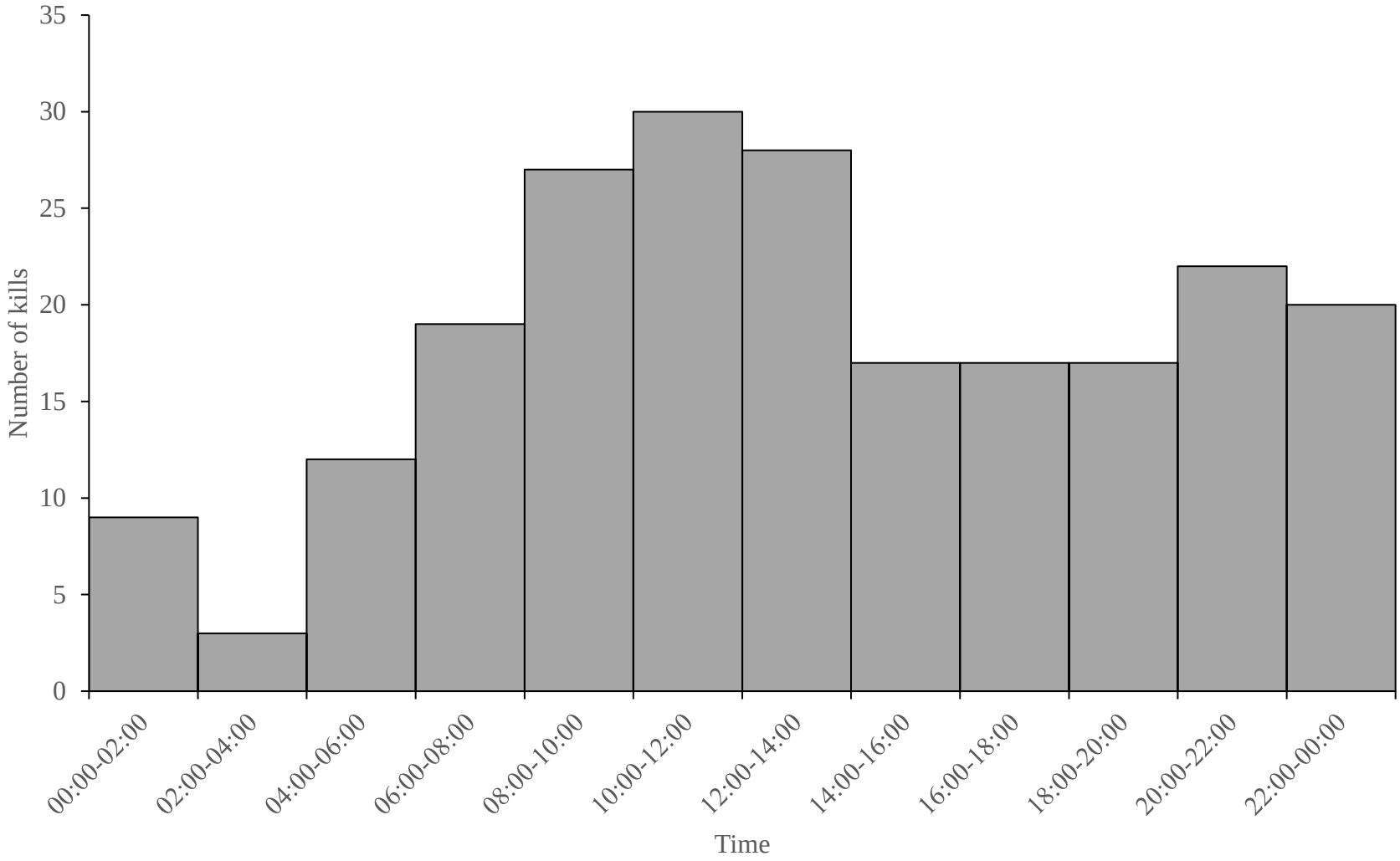

Figure 3. The time of day white-tailed deer (*Odocoileus virginianus*) fawns were killed by 12 wolves (*Canis lupus*) during 2016–2019 in Minnesota, USA.

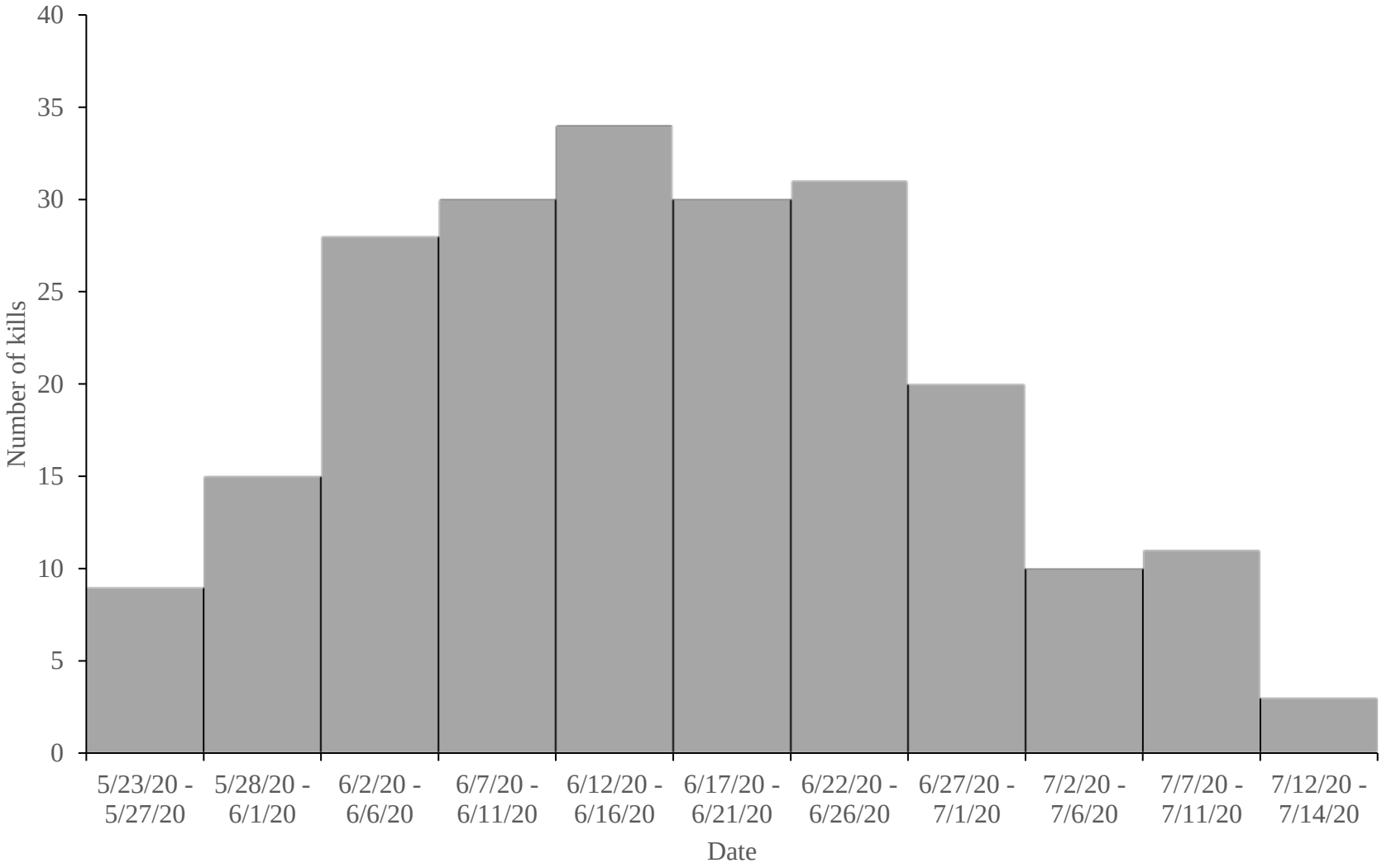

Figure 4. The dates white-tailed deer (*Odocoileus virginianus*) fawns were killed by wolves (*Canis lupus*) in 2016–2019 in Minnesota, USA.

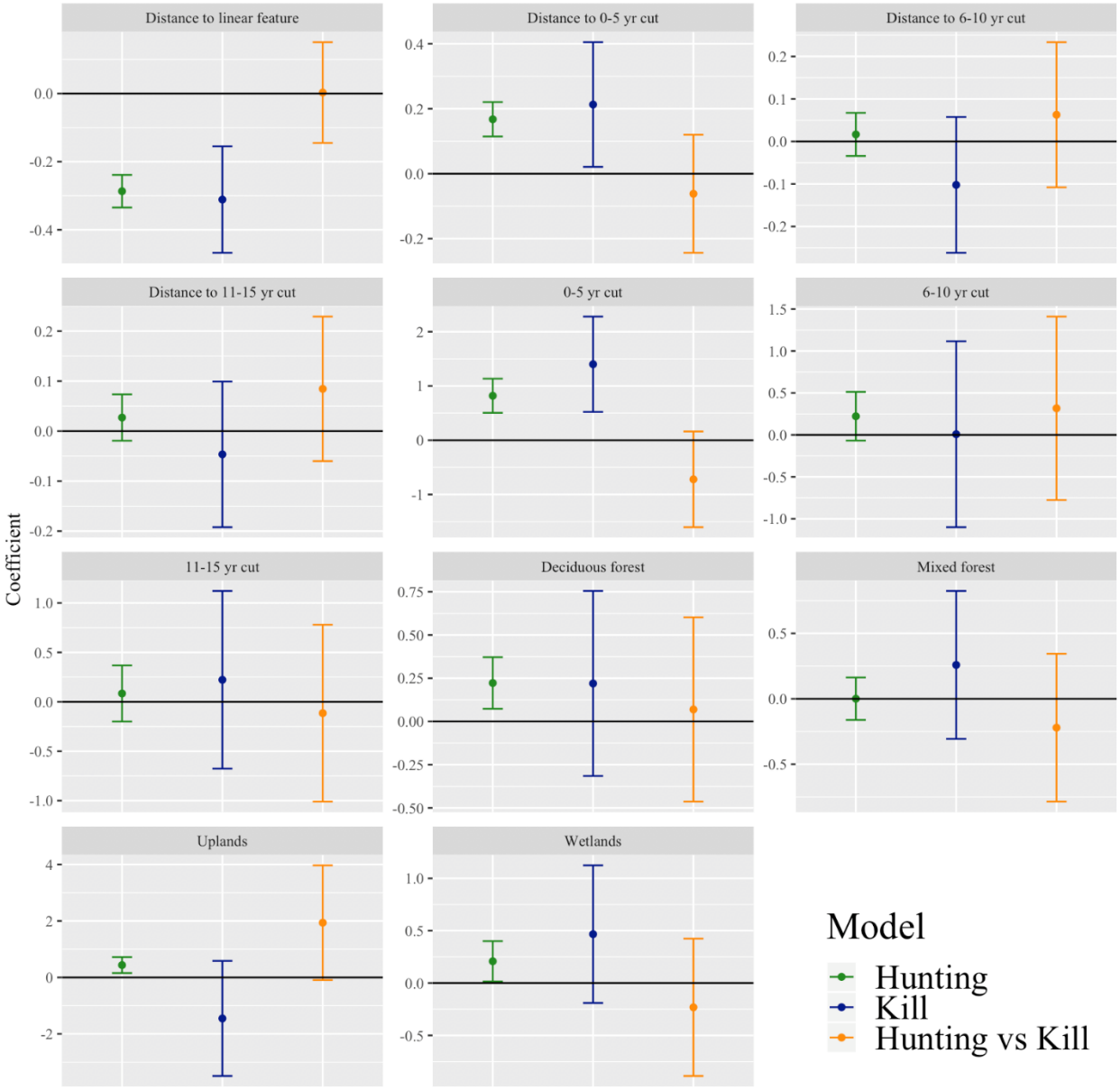

Figure 5. Coefficients for covariates used in 3 logistic regression models for where wolves (*Canis lupus*) hunted white-tailed deer (*Odocoileus virginianus*) fawns (in green), killed deer fawns (in blue), and a comparison of where wolves hunted and killed fawns (in orange) in 2016–2019 in northerm Minnesota, USA.

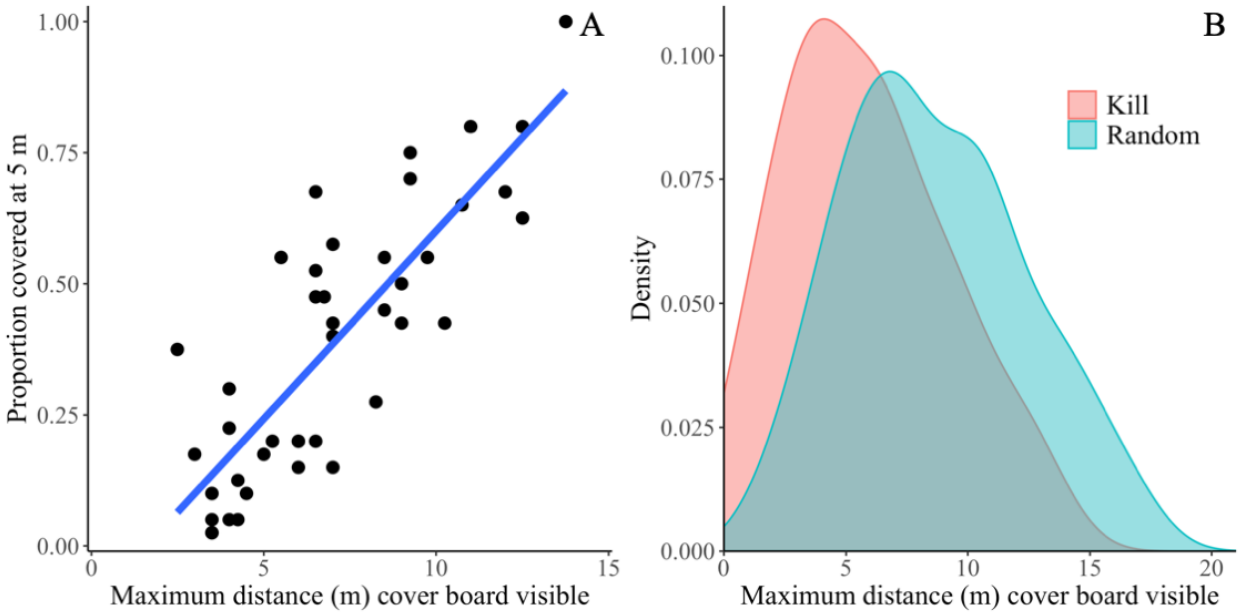

Figure 6. (A) The correlated relationship (r = 0.832) between the amount of a 30.5 x 10 cm cover board that was visible when placed on the ground and viewed from 1 m above the ground from a distance of 5 m at sites where wolves (*Canis lupus*) killed fawns (*Odocoileus virginianus*) and random locations and the maximum distance (m) the board could be seen at the same sites. Measurement were also taken at 10 and 15 m from the board (not shown) and were all correlated. (B) Comparison of the farthest distances (m) a 30.5 x 10 cm cover board was visible at sites where wolves killed fawns ($\bar{x}$ = 5.8 m SD = 3.4) and random locations ($\bar{x}$ = 8.7 m SD = 3.7).

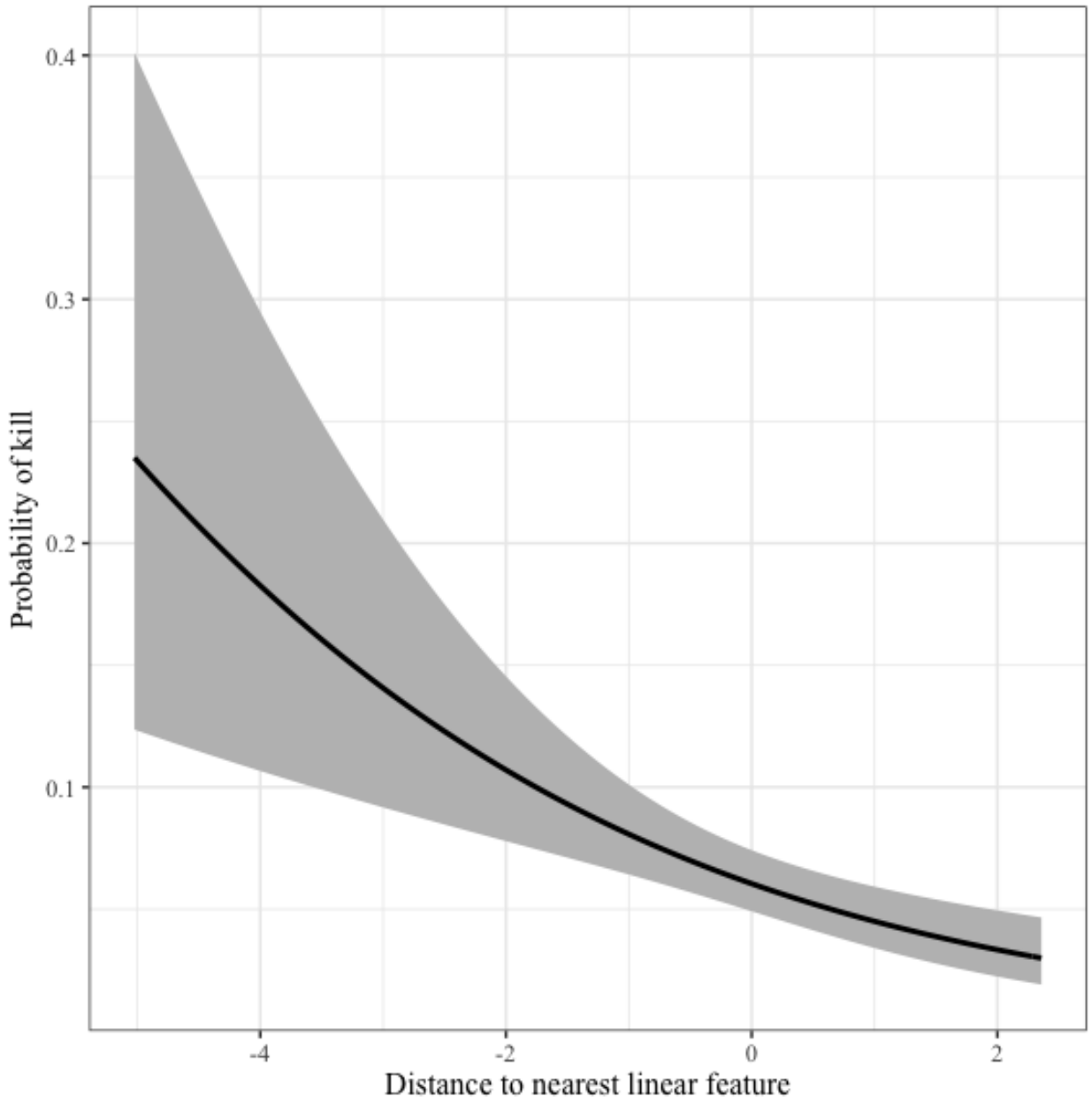

Figure 7. The relationship between the normalized distance from a given location to the nearest anthropomorphic linear feature and the probability the location is a site where a wolf (*Canis lupus*) killed a white-tailed deer fawn (*Odocoileus virginianus*) calculated using a generalized linear mixed model (GLMM). The confidence interval is shaded in gray. As the normalized values approach -4, the distances to the nearest linear feature approach 0 m and as the normalized values approaches 2 the distance to the nearest linear feature approaches 3,475 m.

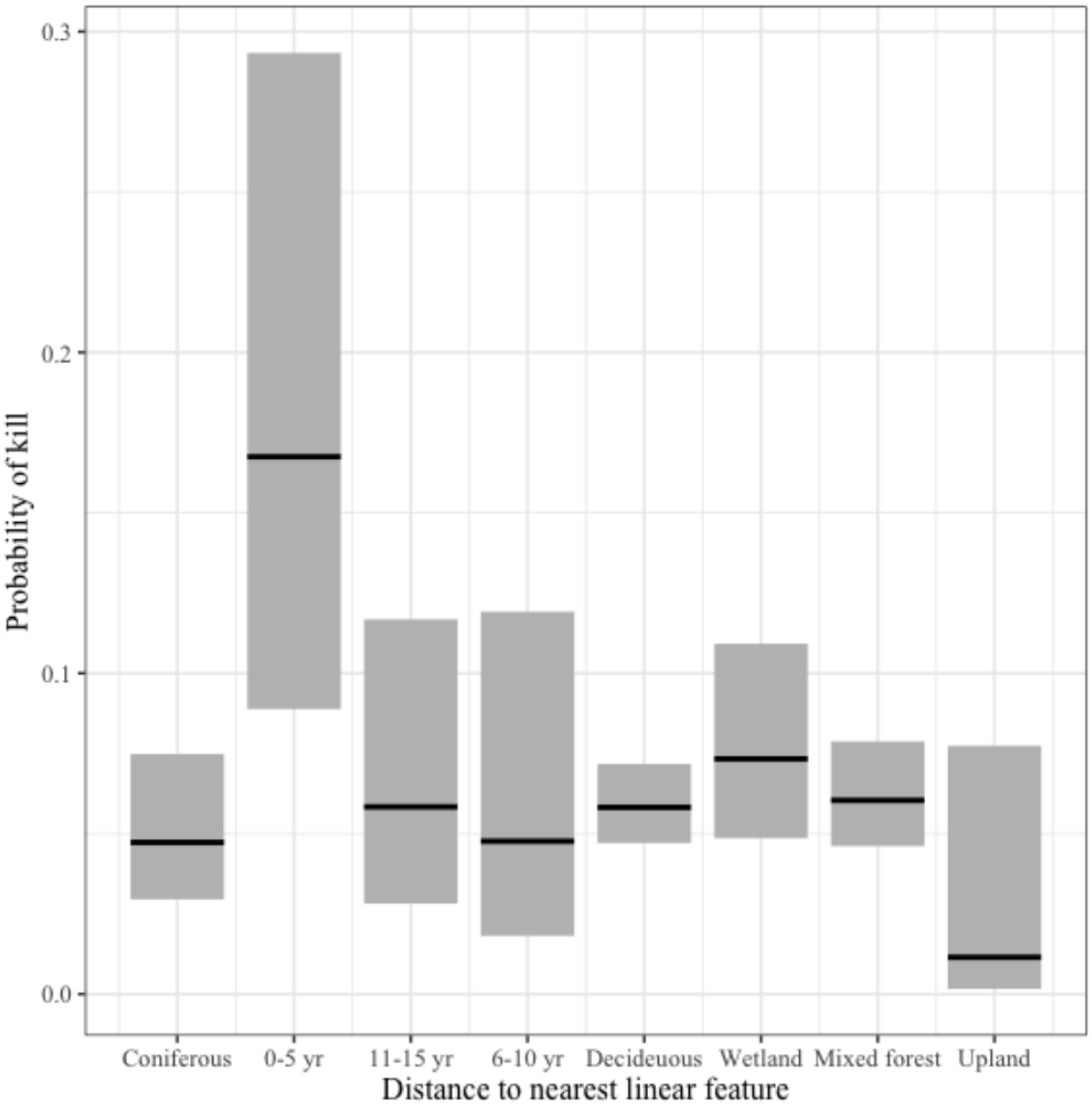

Figure 8. The probability that a location in a site where wolves (*Canis lupus*) killed a white-tailed deer fawn (*Odocoileus virginianus*) in different cover types in northern Minnesota calculated using a generalized linear mixed model (GLMM). The confidence interval is shaded in gray. Coniferous forest was used as a reference variable. Cover types 0–5 yr, 11–15 yr, and 6–10 yr, were named after the number of years since a given patch was cleared of trees as a result of timber harvest.

APPENDIX A

National Park Service Institutional Animal Care and Use Committee (IACUC) approval.

United States Department of the Interior
NATIONAL PARK SERVICE
Biological Resource Division
1201 Oakridge Drive, Suite 200
Fort Collins, Colorado 80525

National Park Service
Institutional Animal Care and Use Committee
Animal Research Protocol Approval

Principal Investigator(s): Steve Windels
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Region: MWR

Protocol Approval Number: MWR_VOYA_Windels_Wolf_2015.A3
Project Title: Investigations of Wolf Ecology in Voyageurs National Park

Approval Date: 5/21/15
Effective Date: 5/21/15

Questionnaire Dates; Years 1 and 2 (if applicable): 5/21/16, 5/21/17

Expiration/Re-Submittal Date: 5/21/18

Funding Agency(ies): NPS, University of Minnesota-Duluth

Species: *Canis lupus*- Gray Wolf

Number(s) of Animals: <20 per year

This project study was reviewed by the National Park Service Institutional Animal Care and Use Committee. The following action(s) were taken:

Project Status: Approved

Interim NPS IACUC Chair: /s/ Tim Pinion; **Date**: 5/21/15
NOTE: Immediately report any/all unexpected mortalities to the NPS IACUC as you would to your primary, approving IACUC of record.